Modeling the kinematics of the canine midcostal diaphragm

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Amancharla, Maneesh R., Joseph R. Rodarte, and Aladin M. Boriek. Modeling the kinematics of the canine midcostal diaphragm. Am J Physiol Regulatory Integrative Comp Physiol 280: R588–R597, 2001.—The hypotheses that the chest wall insertion (CW) is displaced laterally during inspiration and that this displacement is essential in maintaining muscle curvature of the costal diaphragmatic muscle fibers were tested. With the use of data from three dogs, caudal, lateral, and ventral displacements of CW during both quiet, spontaneous inspiration and during inspiratory efforts against an occluded airway were observed and recorded. We have developed a kinematic model of the diaphragm that incorporates these displacements. This model describes the motions of the muscle fibers and central tendon; the displacements of the midplane, muscle-tendon junction (MTJ), CW, and center of the muscle fiber-central tendon arcs are modeled as functions of muscle fiber length. In the model, the center of the fiber arcs and MTJ both move caudally parallel to the midplane during inspiration, whereas CW moves both caudally and laterally. The observed lateral displacement of CW and the observed caudal displacement of MTJ, as functions of muscle fiber length, both approximate well the theoretical displacements that would be necessary to maintain curvature of the fiber arcs. In confirming our hypotheses, we have found that lateral displacement of CW is a mechanism by which changes in the shape of the costal diaphragm, as described by its curvature, are limited.

Respiratory mechanics; chest wall; muscle

WE HAVE PREVIOUSLY shown that the muscle fibers (MFs) of the active canine midcostal diaphragm form arcs of circles whose curvature varies little in the physiological range of lung volumes, i.e., from functional residual capacity (FRC) to end of inspiratory effort at total lung capacity (TLC) (3, 4). Given that the MFs contract by ~35% of their length in the physiological range, some mechanisms are at work by which the diaphragm maintains shape. These mechanisms, however, are poorly understood. Whereas a previous study showed that diaphragm shape is maintained as a pressurized membrane due to muscle anisotropy and central tendon (CT) inextensibility (2), another mechanism is sought because anisotropy does not fully explain the effects of muscle shortening and activation on diaphragm shape. This study examines displacement of the chest wall insertion (CW) as a mechanism that limits changes in diaphragm shape during inspiration.

It is useful first to consider the mechanical properties of the diaphragm. The MFs and CT, which together comprise the diaphragm, form a thin, dome-shaped sheet: a membrane (8). As a pressurized membrane, the diaphragm cannot carry bending moments or compressive stresses in its plane; continuity of slope on the diaphragm surface is therefore expected. The only significant stresses that the diaphragmatic membrane could carry are tensile and shear stresses in the plane of its surface. Maintenance of diaphragm shape also supports the likely scenario of uniformity in stress along the length of an MF. The CT is essentially isotropic and inextensible within the range of physiological stresses imposed on it (2).

A number of assumptions regarding the shape and motion of the diaphragm must also be made when modeling its motion. First, it should be emphasized that only the midcostal region of a hemi-diaphragm is being modeled and that any assumptions made do not necessarily extend to the dorsal costal or crural regions of the diaphragm. The diaphragm exhibits uniform motion during inspiration. The MF bundles lie along curved lines and attach to CW and CT. The MFs contract during inspiration, generating stresses parallel to their length. Each MF arc moves in its own best-fit plane of maximum curvature during inspiration (1), and the centers of the circles associated with these arcs move along a specific trajectory (the nature of this trajectory will be discussed). Because MFs lie along lines of maximum principal curvature of the surface of the diaphragm, the terms “in the direction of an MF” and “in an MF’s plane of maximum curvature” are similar (the former is a line in the plane of the latter). Planes of maximum curvature for different MFs need not be parallel to each other, although they do appear to be parallel for adjacent muscle bundles in the midcostal diaphragm (3, 4).

In the midcostal region, the curvature of the diaphragm transverse to the MFs is not significantly different from zero. Boriek et al. (4) have illustrated this property by orienting adjacent midcostal MFs in their own planes of maximum curvature; as a result, the

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fibers appear to be superimposed on each other at any lung volume during inspiration. Thus adjacent midcostal MFs together form a section of a cylinder whose long axis is parallel to the CW insertion (1, 3).

Although more physiologically accurate than previous models of diaphragm motion (5–7), the model of diaphragm kinematics proposed by Boriek et al. (3) did not consider certain properties of the diaphragm, most notably, displacement of the CW. In this paper, we propose a model of costal diaphragm kinematics expanded from that of Boriek et al. (3). This model includes lateral displacement of CW as an essential mechanism by which changes in the shape of the active midcostal diaphragm, as described by its muscle fiber curvature, are limited.

METHODS

Three bred-for-research beagle dogs, weighing between 9.9 and 10.5 kg, were surgically prepared using the same methods that were used in an earlier study (1). The abdomen was opened by midline laparotomy, and 2-mm silicon-coated lead spheres were stitched to the peritoneal surface of muscle bundles in the midcostal region of the left hemidiaphragm and to the peritoneal surface of CT along the midline (Fig. 1). Four markers were placed along each of three nearby muscle bundles: one at the origin of each muscle bundle on CT ("muscle-tendon junction (MTJ) marker"), one at its insertion on CW ("CW marker"), and two at equal intervals along the muscle bundle. Seven markers were stitched to CT along the midline from the sternum to the spine ("midplane markers"). The animals were allowed to recover from the surgery for at least 3 wk.

The animals were anesthetized with pentobarbital sodium (30 mg/kg), intubated with a cuffed endotracheal tube, and placed in the supine or prone posture in a radiolucent body plethysmograph that was situated in the test field of a computer-based biplanar videoroentgenographic recording system. This high spatial (±0.5 mm) and temporal (30 Hz) resolution system was used to record displacements of the radiopaque metallic markers. Balloon-tipped catheters were inserted in the stomach and esophagus. The positions of the catheters were checked by fluoroscopy and by demonstrating that abdominal pressure increased and esophageal pressure decreased during a spontaneous breath and that esophageal and airway pressures decreased equally during an occluded inspiratory effort at FRC. Biplanar images were recorded continuously during five spontaneous breaths. The lungs were then inflated and occluded successively at various lung volumes. The airway was held occluded until the animal made inspiratory efforts against the occluded airway. Biplanar images were recorded when the change of airway pressure reached a plateau, usually during the fifth or sixth inspiratory effort at each lung volume. The animal was then rotated to the opposite posture, and the procedure was repeated.

We therefore investigated both 1) quiet, spontaneous, open-airway breathing (i.e., normal lung volume expansion occurs) and 2) spontaneous inspiratory efforts against an occluded airway (i.e., lung volume held constant). "Inspiration" thus refers both to quiet, spontaneous breathing and to inspiratory efforts against an occluded airway, both of which are included in our data. During the quiet, spontaneous breathing maneuvers, images were captured at two lung volumes: end of expiration (EE) and end of inspiration (EI). Similarly, during the occluded airway maneuvers, images were captured at the end of inspiratory effort at three occluded lung volumes: FRC, FRC + one-half inspiratory capacity (IC), and TLC.

The coordinates of the lead spherical markers in the two biplanar images were determined, and the three-dimensional coordinates of the markers were computed at all lung volumes. The length of each muscle bundle in each state was determined by the distances between markers on each bundle, and the average length of each of the three bundles across five consecutive efforts was computed. This incremental linear fit to the curved muscle bundle is valid because muscle bundles form smooth arcs, and the four markers on a muscle bundle were placed only 1–2 cm apart. The position of the markers relative to the muscle is ensured because muscle bundles form smooth arcs, and the four markers on a muscle bundle were placed only 1–2 cm apart. Finally, at the end of the experiment, the diaphragm was excised and the configuration of the markers was confirmed visually.

A plane was fit through the locations of the 12 markers in the midcostal diaphragm at occluded TLC. This plane was used as the basis for a local $\xi$-$\eta$-$\zeta$ coordinate system in which the data for all lung volumes for a given dog and posture were viewed (Fig. 2). The plane of maximum curvature of these 12 markers was computed and defined as the $\eta$-$\zeta$ plane. The midplane of the dog was determined by fitting a plane through the locations at TLC of the seven markers stiched along the midline on CT. The $\eta$-$\zeta$ axes were rotated in their own plane to align the $\zeta$-axis with the midplane of the dog. The $\xi$-axis is perpendicular to the $\eta$-$\zeta$ plane. The data from all lung volumes for a given dog and posture were then transformed to the $\xi$-$\eta$-$\zeta$ coordinate system and viewed in the $\eta$-$\zeta$ plane. In the midcostal region of the diaphragm, positive values of $\xi$ and $\eta$ are only slightly different from the conventional anatomic coordinates “ventral” and “lateral,” respectively, and will be referred to as such. Positive $\zeta$ will be referred to as cranial, and negative $\zeta$ will be referred to as caudal.

Displacements of CW, MTJ, and midplane markers both in and out of the plane of maximum curvature ($\eta$-$\zeta$ plane) were examined. Of the seven midplane markers, we excluded the three most dorsal and the single most ventral markers and considered only the three remaining markers because they were closest to a continuation of the midcostal MFs. These

![Fig. 1. Locations of metallic markers on abdominal surface of left midcostal diaphragm and midplane. Four markers were sutured along each of 3 muscle bundles from the origins of the bundles on the central tendon (CT) to their insertions on the chest wall (CW). Seven additional markers were sutured to the midplane of the diaphragm: 4 on the costal diaphragm, 3 on the crural. MTJ, muscle-tendon junction.](http://ajpregu.physiology.org/))
three markers were then used to calculate the displacement of the midplane.

The data analyzed in this study were originally obtained from experiments in a previously published work (3). However, the majority of the data used for this study was not considered in that earlier work. The earlier work analyzed displacements of the MF and MTJ but dismissed displacements of CW as negligible; this study focuses on the displacements of CW. Also, data from the midplane markers on the CT are considered for the first time in this study.

RESULTS

Displacements and equations. We have observed the motion of the CW, MTJ, and midplane markers during inspiration. Visual inspection of the data reveals that the insertion on CW is not fixed. Further mathematical analysis of the markers confirms displacements of CW, MTJ, and the midplane during inspiration. Displacements for each posture along each coordinate axis are recorded from the midcostal CW markers (Fig. 3), from the midcostal MTJ markers (Fig. 4), and from the midplane markers (Fig. 5). The displacements in these figures represent displacements from EE to EI during quiet, spontaneous breathing, from EE to spontaneous effort at an occluded lung volume of FRC, from EE to spontaneous effort at occluded FRC + one-half IC, and from EE to spontaneous effort at occluded TLC.

We have best fit a line through the data points in displacement plots of CW, MTJ, and midplane versus normalized muscle length $\gamma$ ($\gamma = 1$ at EE), considering displacements on each axis separately. Thus equations of CW, MTJ, and midplane displacements as functions of normalized muscle length have been determined and are listed in Tables 1-3 (all numbers are in cm; positive values of $\xi$, $\eta$, and $\zeta$ represent ventral, lateral, and cranial motions, respectively).

Interestingly, the motion of the diaphragm from EE to EI (i.e., from a passive to an active state) appears to be qualitatively different from its motion between active states. Also, the MF markers at EE are fit less well by an arc than the markers at other lung volumes, as can be seen in Fig. 6A, which shows the positions of the diaphragm markers in the $\eta\zeta$ plane for one dog in the supine posture. An observation of the motion of the markers on the diaphragm as it moves from an active to a passive state at the same lung volume suggests that the motion of the diaphragm is quite different.
during that brief transition from an active to a passive state. An inspection of the equations for CW displacement (Table 1) indicates that there is a higher rate of CW displacement with respect to unit MF shortening during that brief transition from an active to a passive state. An inspection of the equations for CW displacement (Table 1) indicates that there is a higher rate of CW displacement with respect to unit MF shortening.
at low lung volumes during the transition from a passive to an active state at the onset of an inspirtory effort. The focus of this paper, however, is the kinematics of the active diaphragm.

Ventral motion. To determine whether the ventral (perpendicular to the plane of maximum curvature of the MFs) displacement of CW represents a uniform ventral displacement of the midcostal diaphragm, the ventral displacements of CW, MTJ, and the midplane are compared: ratio of $D_{MTJ}$ to $D_{CW}$ to $D_{midplane} = 1.78:1.87:1.00$ in the prone posture, and $0.82:2.07:1.00$ in the supine posture, where $D$ is change. Because the ventral displacements of the CW, MTJ, and midplane markers are on the same order of magnitude, it can be inferred that a uniform ventral displacement of the entire diaphragm takes place. Uniform dorsoventral motion of the diaphragm suggests an absence of torsion of the diaphragm surface during inspiration. Teleologically, an absence of torsion increases efficiency because energy is used in displacing the diaphragm rather than wasted in distorting its surface.

MTJ and midplane. Visual inspection of Figs. 3 and 4 suggests that the displacement, on each axis, of the MTJ markers approximates that of the midplane markers. Two-sample $t$-tests (2 tailed, 95% confidence level) confirm that there are no significant differences between the displacements, on any axis, of the MTJ and midplane markers (comparing each posture and lung volume separately).

As shown in Figs. 3 and 4 and in Tables 2 and 3, the motions both of the MTJ and midplane markers are primarily caudal and slightly ventral. We have already examined the ratios of ventral displacements and have found that a uniform ventral displacement of the entire midcostal diaphragm occurs. Examining the ratios of caudal displacements of the MTJ and midplane markers shows only small differences between the two: $\Delta MTJ_z$ to $\Delta midplane_z$ ratio = 1.21:1 (prone) and 1.47:1 (supine). These small differences are partly attributable to the difficulty in stitching precisely, in vivo, the midplane markers onto the hypothetical extension of the diaphragm.

<table>
<thead>
<tr>
<th>Table 1. CW displacement as a function of $\gamma$</th>
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<tr>
<td>Prone</td>
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<tr>
<td>$\Delta CW_y(\gamma)$ = $-3.82\gamma + 3.47$, $R^2 = 0.779$</td>
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<tr>
<td>$\Delta CW_h(\gamma)$ = $-1.42\gamma + 1.39$, $R^2 = 0.869$</td>
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<tr>
<td>$\Delta CW_z(\gamma)$ = $1.27\gamma - 1.08$, $R^2 = 0.623$</td>
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<tr>
<td>Supine</td>
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<tr>
<td>$\Delta CW_y(\gamma)$ = $-390\gamma + 542$, $R^2 = 0.218$</td>
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<tr>
<td>$\Delta CW_h(\gamma)$ = $-2.52\gamma - 2.56$, $R^2 = 0.793$</td>
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Table 2. MTJ displacement as a function of $\gamma$

<table>
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<tbody>
<tr>
<td>$\Delta MTJ_y(\gamma)$ = $-4.02\gamma + 3.96$, $R^2 = 0.820$</td>
</tr>
<tr>
<td>$\Delta MTJ_h(\gamma)$ = $-0.721\gamma + 0.740$, $R^2 = 0.248$</td>
</tr>
<tr>
<td>$\Delta MTJ_z(\gamma)$ = $9.03\gamma - 8.55$, $R^2 = 0.982$</td>
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<tr>
<td>Supine</td>
</tr>
<tr>
<td>$\Delta MTJ_y(\gamma)$ = $-1.33\gamma + 1.21$, $R^2 = 0.965$</td>
</tr>
<tr>
<td>$\Delta MTJ_h(\gamma)$ = $-0.145\gamma + 0.288$, $R^2 = 0.225$</td>
</tr>
<tr>
<td>$\Delta MTJ_z(\gamma)$ = $10.2\gamma - 10.2$, $R^2 = 0.967$</td>
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MTJ, muscle-tendon junction. $\Delta MTJ_y(\gamma)$, ventral displacement of the MTJ; $\Delta MTJ_h(\gamma)$, lateral displacement of the MTJ; $\Delta MTJ_z(\gamma)$, cranial displacement of the MTJ.
an MF on the CT (i.e., intersection of the $\eta$-$\zeta$ plane and the midplane). Moreover, Tables 2 and 3 show that the caudal displacements both of the MTJ (prone: $R^2 = 0.982$; supine: $R^2 = 0.967$) and midplane (prone: $R^2 = 0.991$; supine: $R^2 = 0.992$) are highly regular and predicted well by a linear fit to the data.

There is an absence of consistent lateral/medial displacement as a function of muscle length of both the MTJ (prone: $R^2 = 0.248$; supine: $R^2 = 0.225$) and midplane (prone: $R^2 = 0.063$; supine: $R^2 = 0.685$) markers. Furthermore, a two-sample $t$-test (2-tailed, 95% confidence interval) indicates no significant differences between the lateral displacements of both the midplane and MTJ markers. Thus the trajectory of the MTJ markers during inspiration may be parallel to the midplane.

Figure 6 illustrates the positions and trajectories of the diaphragm markers for one dog in the supine posture. In Fig. 6A, midplane markers at the same lung volume appear to form an arc; this is the case because they were stitched onto the dome-shaped central tendon and are now viewed in the plane of maximum curvature of the MFs, which is not precisely perpendicular to the plane of maximum curvature of the midplane markers on the CT. Thus, although different midplane markers at the same lung volume form an arc, the trajectory of each midplane marker is approximately linear. It is these trajectories that are drawn in Fig. 6A and whose average is shown in Fig. 6B. One can see that the trajectory of the MTJ during inspiration is essentially linear and parallel to the trajectory of the midplane markers; these two linear trajectories form a 7° angle for this dog.

Chest wall. Figure 3 and Table 1 reveal caudal and lateral displacements of the chest wall during inspiration. Although not as linear as the caudal motion of the MTJ and midplane, a linear fit to the caudal displacement of the CW versus muscle length is quite good (prone: $R^2 = 0.623$; supine: $R^2 = 0.793$). The lateral displacement of the CW, however, is only fit well by a line in the prone posture ($R^2 = 0.869$); a linear fit does not predict the data well in the supine posture ($R^2 = 0.218$). Our model of midcostal diaphragm kinematics is thus better supported by the physiological prone posture than by the unphysiological supine posture.

$T$-tests (2-tailed, 95% confidence level) reveal significant differences between the prone and supine postures for all three components of CW displacement and for the ventral and caudal (but not the lateral/medial) components of MTJ displacement. No significant differences have been found between the postures for the midplane displacements.

Kinematic model. In an earlier work, Boriek et al. (4) did observe caudal and lateral displacement of CW, but these displacements were not computed and were not included in the kinematic model of diaphragm mechanics that they later formulated (3). We have computed these CW displacements and incorporated them into a kinematic model of the canine midcostal diaphragm.

Our kinematic model of the midcostal diaphragm is shown in Fig. 7. An MF and its CT extension are shown

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**Table 3. Midplane displacement as a function of $\gamma$**

<table>
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<th>Prone</th>
<th>Supine</th>
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<tr>
<td>$\Delta$Midplane$_{\gamma}$</td>
<td>$3.38\gamma + 3.31, R^2 = 0.692, -0.645\gamma + 0.600, R^2 = 0.810$</td>
<td>$3.04\gamma - 2.71, R^2 = 0.911, 0.755\gamma - 0.676, R^2 = 0.685$</td>
</tr>
<tr>
<td>$\Delta$Midplane$_{\eta}$</td>
<td>$7.45\gamma - 7.18, R^2 = 0.991, 6.92\gamma - 7.15, R^2 = 0.992$</td>
<td>$7.15\gamma - 7.05, R^2 = 0.992, 6.67\gamma - 7.15, R^2 = 0.992$</td>
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**Fig. 6. Locations of the muscle fiber (MF) and midplane markers, for a supine dog, viewed in the $\eta$-$\zeta$ coordinate system (positive $\eta$ is lateral; positive $\zeta$ is cranial). A: the data are shown along with best-fit curves. On the right, an arc of a circle is fit to the MF markers at each lung volume; on the left, a straight line is fit to the trajectory of each of the 4 midplane markers as lung volume changes. B: from the data in A, the best-fit arcs to the MFs at each lung volume are redrawn. The separate trajectories of the 4 midplane markers are combined, and an average midplane trajectory is shown. Additionally, the average CW and MTJ locations at each lung volume and the best-fit line to the MTJ markers are shown. The angle between the trajectories of the midplane and MTJ markers is 7°.**
The model and found experimentally. The model predicted no lateral/medial motion of the MTJ and midplane, and the experimental data confirm this. Finally, the uniform ventral (+z) displacement of the entire diaphragm suggested by the data is not predicted by, but is consistent with, the model.

**DISCUSSION**

*MTR and midplane.* The highly linear, parallel, and approximately equal caudal and ventral motions of the MTJ and midplane, their statistically insignificant lateral/medial motions, and the lack of statistically significant differences among their motions on any axis together suggest that the MTJ should always have the same location relative to a point on the CT that lies on the midplane, provided that both are in the same η-ζ plane. This assertion is also made likely by the inextensibility of the CT and the fact that points on the CT that are on the midplane at one lung volume probably remain on the midplane at other lung volumes.

The absence of significant lateral/medial motion of the midplane markers is also predicted by the mechanical properties of the diaphragm: lateral/medial motion of the midplane would require either torsion of the diaphragm surface or asymmetry in the motions of the left and right hemidiaphragms. If the midplane were to move laterally for MFs in one hemidiaphragm, it would move medially for MFs in the other hemidiaphragm. But if CW were fixed and if curvature in the direction of an MF were maintained, this phenomenon could occur only if the angle subtended by the MF and CT from CW to midplane is <90° in one hemidiaphragm and >90° in the other. This asymmetry, in which the midcostal MFs are of different lengths in opposite hemidiaphragms and in which the midplane follows different trajectories in different fibers’ planes of maximum curvature, is unlikely.

*Chest wall.* A fixed CW is inconsistent with the kinematics and mechanics of the canine midcostal diaphragm. Key assumptions regarding the kinematics and mechanics are that 1) the MF arcs maintain similar shape during inspiration, 2) the MTJ always has the same location relative to a point on the CT that lies on the midplane and in the same η-ζ plane, 3) slope and curvature are continuous at the MTJ, and 4) points on the CT that are on the midplane remain on the midplane at all lung volumes during inspiration. If these assumptions are valid, a simple geometrical analysis shows that the centers of the circles associated with an MF were maintained, this phenomenon could occur only if the angle subtended by the MF and CT from CW to midplane is <90° in one hemidiaphragm and >90° in the other. This asymmetry, in which the midcostal MFs are of different lengths in opposite hemidiaphragms and in which the midplane follows different trajectories in different fibers’ planes of maximum curvature, is unlikely.

The absence of significant lateral/medial motion of the midplane markers is also predicted by the mechanical properties of the diaphragm: lateral/medial motion of the midplane would require either torsion of the diaphragm surface or asymmetry in the motions of the left and right hemidiaphragms. If the midplane were to move laterally for MFs in one hemidiaphragm, it would move medially for MFs in the other hemidiaphragm. But if CW were fixed and if curvature in the direction of an MF were maintained, this phenomenon could occur only if the angle subtended by the MF and CT from CW to midplane is <90° in one hemidiaphragm and >90° in the other. This asymmetry, in which the midcostal MFs are of different lengths in opposite hemidiaphragms and in which the midplane follows different trajectories in different fibers’ planes of maximum curvature, is unlikely.

Circular trajectories, however, are inconsistent with the physiological data; it has already been shown that the trajectories of the MTJ and midplane are highly linear (R^2 > 0.96 for both and for both postures) and parallel during inspiration.

Moreover, if CW were fixed, at least one of the key assumptions stated above must be violated (Fig. 8). Although either would allow the other key assumptions to remain valid, discontinuities of slope in the CT
65% of its length at FRC. Looking at the relationship between diaphragm curvature and midplane, MTJ, and CW displacements, we see that CW must move laterally for the trajectories of the MTJ and midplane to be essentially linear and parallel. The observed lateral displacement of CW supports this assertion (discussed in Fig. 9).

As the angle subtended by the MF and CT falls below 90° (a lung volume just greater than TLC), medial, rather than lateral, displacement of CW would be required to maintain diaphragm shape. Although this phenomenon has not been observed physiologically, the expected decrease in the rate of lateral CW displacement with respect to muscle shortening as the lung volume approaches TLC has been observed visually.

Kinematic model. Considering a CW that moves laterally during inspiration allows us to test the hypothesis that lateral motion of CW is essential in maintaining diaphragm shape. To maintain curvature of the MF arcs, the kinematic model in Fig. 7 predicts that the lateral component of CW displacement as a function of normalized muscle length \( \Delta CW_n(\gamma) \) must be

\[
\Delta CW_n(\gamma) = R[\cos(\gamma \theta_{EE} + \phi - \pi/2)] - \cos(\theta_{EE} + \phi - \pi/2)
\]

where \( R \) is the radius of curvature of the MF, \( \gamma \) is normalized MF length (\( \gamma = 1 \) at EE), \( \theta_{EE} \) is the angle spanned by the MF at EE, and \( \phi \) is the angle spanned by the CT.

Equation 1 is found from a simple geometrical analysis of the model in Fig. 7: \( R \times \cos(\gamma \theta_{EE} + \phi - \pi/2) \) is simply the distance of CW from the midplane at EE, whereas \( R \times \cos(\theta_{EE} + \phi - \pi/2) \) is the distance of CW from the midplane when the MF has contracted to \( \gamma \) times its length at EE. The difference between these

Fig. 9. Lateral \((\eta)\) displacement of the CW vs. normalized MF length \((\gamma)\). The dotted lines represent the theoretical (theor) range of \( \Delta \eta \) as a function of muscle length, predicted by the model of Fig. 7. Both of the model functions assume that the radius of curvature \((R)\) of the MF arcs is 5 cm and that the angle spanned by the MF at EE is 69°. The upper model limit assumes a CT angle of 46°; the lower is assumed to be 40°. Both of these CT angles are within the physiological range. The same data used in Fig. 3 and Table 1 provide the experimental data points shown.
two terms is the lateral displacement of CW from its location at EE.

With the availability of both model predictions (Eq. 1) and physiological measurements (Fig. 3, Table 1) of the lateral chest wall displacement \(\Delta CW_{\gamma}(\gamma)\), it is useful to compare the lateral displacement observed with that predicted by the model to maintain curvature in the diaphragm (Fig. 9). Because the theoretical lateral displacement that would be necessary depends on the radius of the MF-CT arc and on the angles subtended by the MF and CT, a reasonable range of expected displacement can be generated through the observed physiological range. As per the observations of an earlier study (3), we chose 5 cm to be the radius of the MF-CT arc and 69° to be the angle subtended by the MF at EE. The angle subtended by the CT, which is assumed to be constant in our model, was found to vary between 36° and 53° in that study. Consequently, we constructed a range of expected lateral displacement of CW based on a 6° range of freedom in the length of the CT: 40°–46°. The physiological data fit very well inside the theoretical envelope of displacement that is predicted by the model to maintain curvature.

Although the marker data from both postures support the model, the supine posture produces markedly less consistent results than the prone. Figure 9 shows that the lateral displacement of CW in the supine posture is less than that necessary to maintain diaphragm curvature. Moreover, the low \(R^2\) values for \(\Delta CW_{\gamma}(\gamma)\) in the supine posture (\(R^2 = 0.218\)) confirm that for the supine posture, lateral CW displacement is not predicted well by normalized muscle length. Thus our model of midcostal diaphragm kinematics describes more accurately the physiological prone posture than the unphysiological supine posture.

The same comparison can be made between model predictions and physiological measurements of the caudal displacement of the MTJ with respect to CW as a function of muscle length \(\Delta MTJ_{\gamma}(\gamma) - \Delta CW_{\gamma}(\gamma)\). To maintain diaphragm curvature, our kinematic model predicts that the caudal displacement of MTJ with respect to CW must be

\[
\Delta MTJ_{\gamma}(\gamma) - \Delta CW_{\gamma}(\gamma) = R[\sin(\theta_{EE} + \phi - \pi/2) - \sin(\gamma\theta_{EE} + \phi - \pi/2)] \tag{2}
\]

Equation 2 is derived using a similar geometrical analysis as that used in deriving Eq. 1. Making similar assumptions to those that were made in Fig. 9, Fig. 10 compares the caudal displacement of MTJ that is predicted by the model to that which was observed. The observed caudal displacement is only slightly greater than that predicted by the model. Thus, when Figs. 9 and 10 are considered, the kinematic model is able to predict both the lateral displacement of CW and the caudal displacement of the MTJ based on the assumption that diaphragm shape is maintained. We believe that the data confirm, to a great extent, our hypothesis that lateral displacement of CW is crucial in limiting changes in shape of the active midcostal diaphragm.

**Perspectives**

Diaphragm activation has an inspiratory effect on the rib cage by increasing abdominal pressure, thereby leading to lateral displacement of the CW in the midcostal region of the diaphragm. This study has shown that such displacement of the CW, in turn, acts to limit changes in shape of the active diaphragm. We have developed a kinematic model of the canine midcostal diaphragm that demonstrates the effect of chest wall displacement on diaphragm curvature. The data have confirmed our hypothesis that significant lateral displacement of CW occurs and is an essential mechanism by which changes in the shape of the midcostal diaphragm are limited. The kinematic model includes the lateral and caudal motion of CW during inspiration and describes these displacements as functions of MF length. These functions are based on physiological data that approximate well the lateral displacements predicted by the kinematic model that would be necessary to maintain curvature in the MF arcs. Model predictions of the motion of the MTJ caudally and parallel to the midplane during inspiration are also consistent with the physiological data.

It would also be interesting to examine whether the kinematic model holds for the dorsal region of the costal diaphragm as well as the midcostal. Because our markers were placed only on the midcostal diaphragm, they do not reveal the kinematics of the dorsal region. Because the dorsal region is closer to the crural diaphragm, the kinematics of the dorsal region might be influenced by the mechanics and activation of the crural diaphragm. For example, the crural is stimulated earlier than the costal diaphragm, and the dorsal costal diaphragm might be more affected by that activation. Further study of the dorsal region could reveal whether CW expansion is a
primary mechanism by which shape is maintained in the dorsal costal diaphragm as well.

Although this study has developed a kinematic model of the diaphragm that is valid both for quiet, spontaneous breathing and for inspiratory efforts against an occluded airway, it is difficult to speculate on the applicability of this model to exercise conditions because of different levels of activation of the diaphragm and of the intercostal muscles. It would therefore be useful to test the extensibility of this model to exercise conditions with data gathered from exercising dogs.

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